Dispersal of *Rana temporaria* tadpoles in large fishponds

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Dispersal of *Rana temporaria* tadpoles was monitored from hatching to metamorphosis by systematic sampling at regularly distributed points of two large fishponds in the Jurassian Bresse (Eastern France). Dispersal showed two successive phases. During the first phase, shoals of tadpoles dispersed from the breeding site towards different directions. Then, the shoals spread out and the tadpoles colonized the shallower parts of the pond. They did not colonize the entire pond banks but only the shallower ends, i. e. the largest shallow areas occupied by a high density of vegetation. They emerged on the side of a pond that was the shadiest. Despite great differences in vegetation, mode and dynamics of tadpole dispersal did not differ between the two ponds.

INTRODUCTION

The question of tadpole dispersal is not very well documented. The literature has been mainly concerned with the diel pattern of distribution in small ponds (BEISWENGER, 1977, in *Bufo americanus*; GRIFFITHS, 1985, in *Rana temporaria*). The diel patterns observed in these two species are similar and may be summarized as follows: during the morning, the tadpoles migrate from the deepest zone of the pond towards the banks and aggregate in the shallow areas while temperature is increasing; at dusk, they return to the deepest parts of the pond. ANGELIER & ANGELIER (1968) noted aggregations of tadpoles of *Rana temporaria* on the banks during sunny days. As suggested by these observations, this diel cycle is probably thermo-dependent. Whereas water temperatures reach highest values along the bank during the day, during the night they are highest at the bottom. However, *R. temporaria* tadpoles may move from warmer to cooler water during dispersal (GRIFFITHS & MYLOTTE, 1986)

Tadpole social behaviour during the entire larval period has been described qualitatively in *R. temporaria* by SAVAGE (1961) and GUYÉTANT (1975). According to the latter, tadpoles are gregarious after hatching. They stay for one week at the spawning site where they feed on the gelatinous envelopes of the clutches They remain near the banks at less than 10 cm depth and disperse in the whole pond at the age of twelve to fifteen days, three months after hatching, they come back towards the banks and form aggregations

before metamorphosis. According to SAVAGE (1961), *R. temporaria* tadpoles may remain gregarious for three to six weeks; they then disperse into several separate shoals, apparently based on food resources; eight to nine weeks after hatching they have a solitary life characterized by few feeding movements. These studies were carried out in small fishfree ponds

The surface of the pond and the diversity of its microhabitat probably influence tadpole dispersal. The previous observations concerned only small ponds where tadpoles may wander quickly throughout the pond Dispersal has not been described in large ponds such as fishponds with a surface of several hectares, which provide a higher diversity of microhabitats. Our purpose is to describe precisely the dispersal of tadpoles of *Rana temporaria* during the whole larval period and during froglet emergence in two large fishponds that attract a very large number of breeders (JOLY, 1991, AUGERI & JOLY, 1993) This monitoring was based on systematic sampling of tadpoles at points regularly distributed in the two fishponds.

MATERIAL AND METHODS

STUDY SITES

The two fishponds are located 9 km apart in Jurassian Bresse (Jura Department, between Lons-le-Saulnier and Dôle, altitude 200-215 m). Jurassian Bresse is a mosaic of deciduous forests (*Quercus, Fraxinus* and *Carpinus*), crops, meadows and fishponds devoted to carp farming. These ponds are dried every winter and filled again with rain or brook water. A 1.5 to 3 m deep central ditch leads to a draining point at the deepest end (3 m deep maximum) of each pond. The opposite bank has one or several shallow "tails". Average pond depth is about 0.7 m. Adult *Rana temporaria* usually breed in a tail. Daguin fishpond (3 ha) is surrounded by cultivated lands and meadows. Its tail is adjacent to a little wood. Thévenon fishpond (3.5 ha) is within a forest. Conductivity measured during the spawning period was 161 $\mu S.cm^{-1}$ at Daguin and 34.9 $\mu S.cm^{-1}$ at Thévenon. The higher value at Daguin is due to the proximity of field and pasture. The aquatic vegetation of each pond was mapped during June. Temperature values were regularly recorded at the same hour at several points of the two ponds at a depth of 0.5 m.

SAMPLING MODE

In 1989, *Rana temporaria* tadpoles were collected in the two ponds on five dates regularly distributed over time, from egg hatching to froglet metamorphosis (6 April, 19 April, 4 May, 22 May, 5 June). Samples along transverse transects were taken from a boat. The distance between two successive transects was about 30 m. Samples were uniformly distributed along each transect (about every 40 $\pm$ 5 m) Hence the number of samples per transect varied from five in the wider parts (one in the middle, two near the

banks and two at intermediate points between the middle and the banks) to four and three (middle and banks) in the narrower parts. Sixty-six and seventy-seven points were visited at each date at Thévenon and at Daguin respectively. Three standardized sweeps of a 40 × 40 cm net (0.5 mm mesh) were made at each site from the bottom to the surface. Sampling was always carried out by the same operator. Depth was measured at each sampling point. From 5 to 9 June, we searched the edges of the two fishponds to determine where the froglets left the ponds. Maps of tadpole dispersion were computed using GraphMu on a Macintosh (THIOULOUSE, 1989).

RESULTS AND DISCUSSION

POND DESCRIPTION

The shallowest parts of the ponds (less than 1 m) showed two different shapes. Whereas they were narrow at the lateral banks, they widened out in the tails (fig. 1)

Thirtheen and sixteen macrophyte species were recorded at Thévenon and Daguin respectively (fig. 1). Six species were common to both ponds, *Carex riparia, Glyceria* sp., *Iris pseudacorus, Utricularia vulgaris, Scirpus lacustris* and *Sparganium erectum*. Floating species (*Trapa natans, Potamogeton lucens*) occupied large areas at Daguin but were scarce at Thévenon. The deepest part of Thévenon was covered by Characeae. This plant family was absent at Daguin. The banks were colonized by *Carex* sp. at Thévenon and by *Scirpus lacustris* at Daguin. The communities which occupied the pond tails were different: *Glyceria* sp. and *Carex* sp. were the most frequent at Thévenon, *Sparganium erectum*, *Phragmites australis* and *Typha angustifolia* were the most frequent at Daguin. Daguin is a more eutrophic pond than Thévenon. Vegetation richness at Daguin probably is a consequence of enrichment in mineral salts due to field drainage. Light levels were also higher at Daguin.

Mean temperature values were not significantly different between tails, lateral banks or central parts of the two ponds (two-ways ANOVA, see temperature values in Table I).

TADPOLE DISPERSION

Though beginning earlier at Daguin, tadpole dispersal presented some similarity between the two ponds (fig. 2) The dispersal process went through several phases. About one week after hatching, the tadpoles left the remains of the gelatinous mass. The first tadpoles which were found far from the spawning site were aggregated in some particular points (6 April at Daguin, 19 April at Thévenon). Their first movement was not a diffusion-like dispersal from the spawning site but rather appeared as a group movement of several thousand tadpoles, during about one week. In such shoals, physical contact between tadpoles was frequently observed. After this shoaling movement, tadpoles straggled more widely in the entire pond tails (19 April and 4 May at Daguin, 4 May at

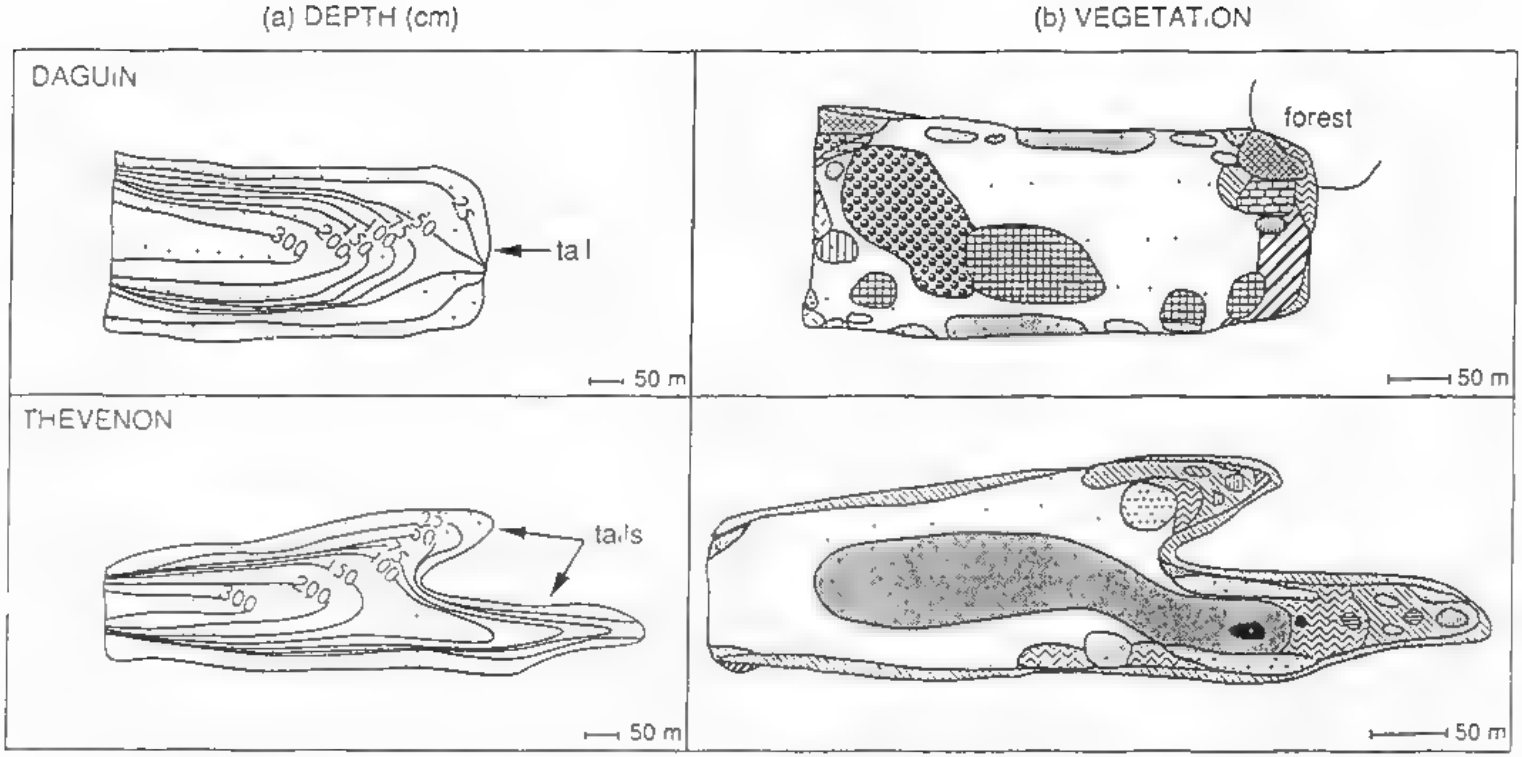

Fig. 1. – (a). Depth isolines in the two ponds the pond tails show a wide area of shallow water. (b) Maps of aquatic vegetation in the two ponds, Daguin and Thévenon. Twenty aquatic plant species have been noted in the two ponds, 16 in Daguin and 13 in Thévenon

Table I. – Temperature mean values (in °C) recorded at each date in the central parts, the lateral banks and the tails of the two ponds.

Dates	Daguin			Thévenon		
	Central parts	Lateral banks	Tails	Central parts	Lateral banks	Tails
6 April	8 6	9 2	9 6	9.2	9.6	10.1
19 April	8.9	9.5	10.1	9 5	9.8	11 0
4 May	12.4	13.6	14.2	14.2	14 8	16 0
22 May	14.5	15.3	16.0	15.5	16 3	17.2
5 June	15.3	16.7	18.2	17.7	18.4	19 5

Thévenon). Physical contact between tadpoles became less frequent. Finally, two months after hatching, they returned to the banks of the tails (22 May) where they emerged (5 June).

In our study, the habitat parameters considered as influencing tadpole distribution were depth, temperature and vegetation. It is clear that tadpoles did not colonize the entire pond but only its shallower parts (< 75 cm) (fig. 3) and did not colonize all the banks but only the ones situated in pond tails (fig. 2). They did not spread out further than 150 m from the spawning site. Previous studies have shown that tadpoles prefer both shallow water and high temperatures (NOLAND & ULTSCH, 1981; FLOYD, 1984; DUPRÉ & PETRANKA, 1985). Tadpole distribution observed in our study may be due to depth rather than to temperature which was on the average not significantly higher in the tails than in the central parts or in the lateral banks of each pond.

Shifts in vegetation occupation occurred during tadpole development in both ponds (fig. 4). At Daguin, at the beginning of April, the tadpoles reached highest densities in *Sparganium erectum*, *Scirpus lacustris* and *Phragmites australis* (6 April). The tadpoles then spread towards patches of *Potamogeton lucens*, *Glyceria* sp and *Utricularia vulgaris* (19 April; 4 May; 22 May). Before metamorphosis (5 June), they occupied only *Sparganium erectum* and *Glyceria* sp. patches. They did not colonize *Trapa natans*, *Potamogeton praelongus* or *Sagittaria sagittifolia*. At Thévenon, at the beginning of the development (6 April), they were found in zones of *Glyceria* sp. Then, whereas some tadpoles remained in *Glyceria* patches, a lot of them shifted (19 April) to patches of *Carex riparia*, *Utricularia vulgaris*, and, to a lesser extent, *Potamogeton pectinatus* and *Scirpus lacustris*. Before metamorphosis, they mainly occupied patches of *Glyceria* sp. and *Carex riparia* (4 June). They avoided Characeae (fig. 4). As a whole, tadpoles mainly inhabited species of shallow water but only those that occupy the tails. Contrarily to the lateral banks, tails constitute large areas of shallow water and of high density of vegetation

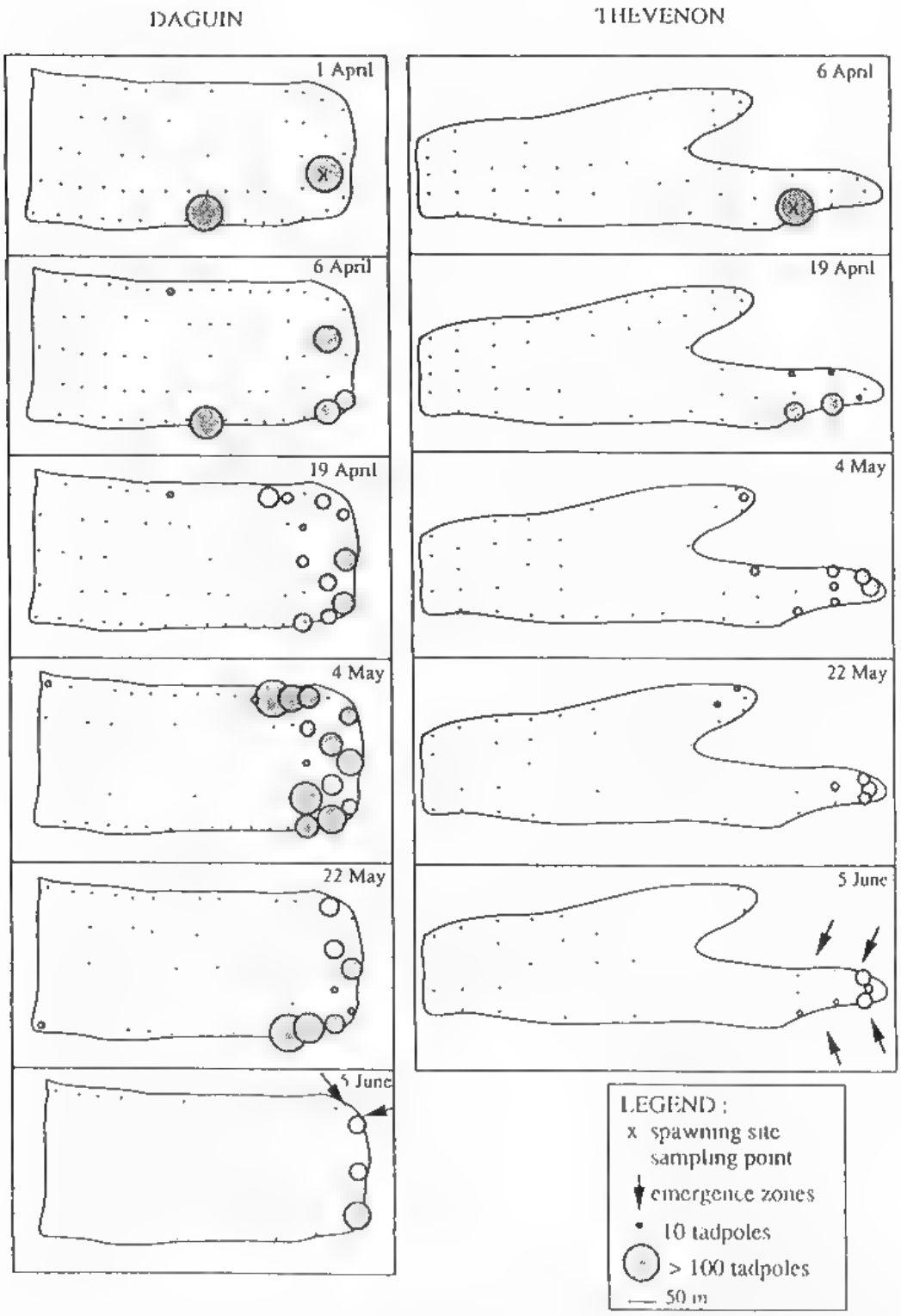

Fig 2 – Dispersion of tadpoles at each sampling date The size of each circle is proportional to the number of tadpoles collected according to a logarithmic scale The size of the circles shown in the legend are given as examples of tadpole numbers

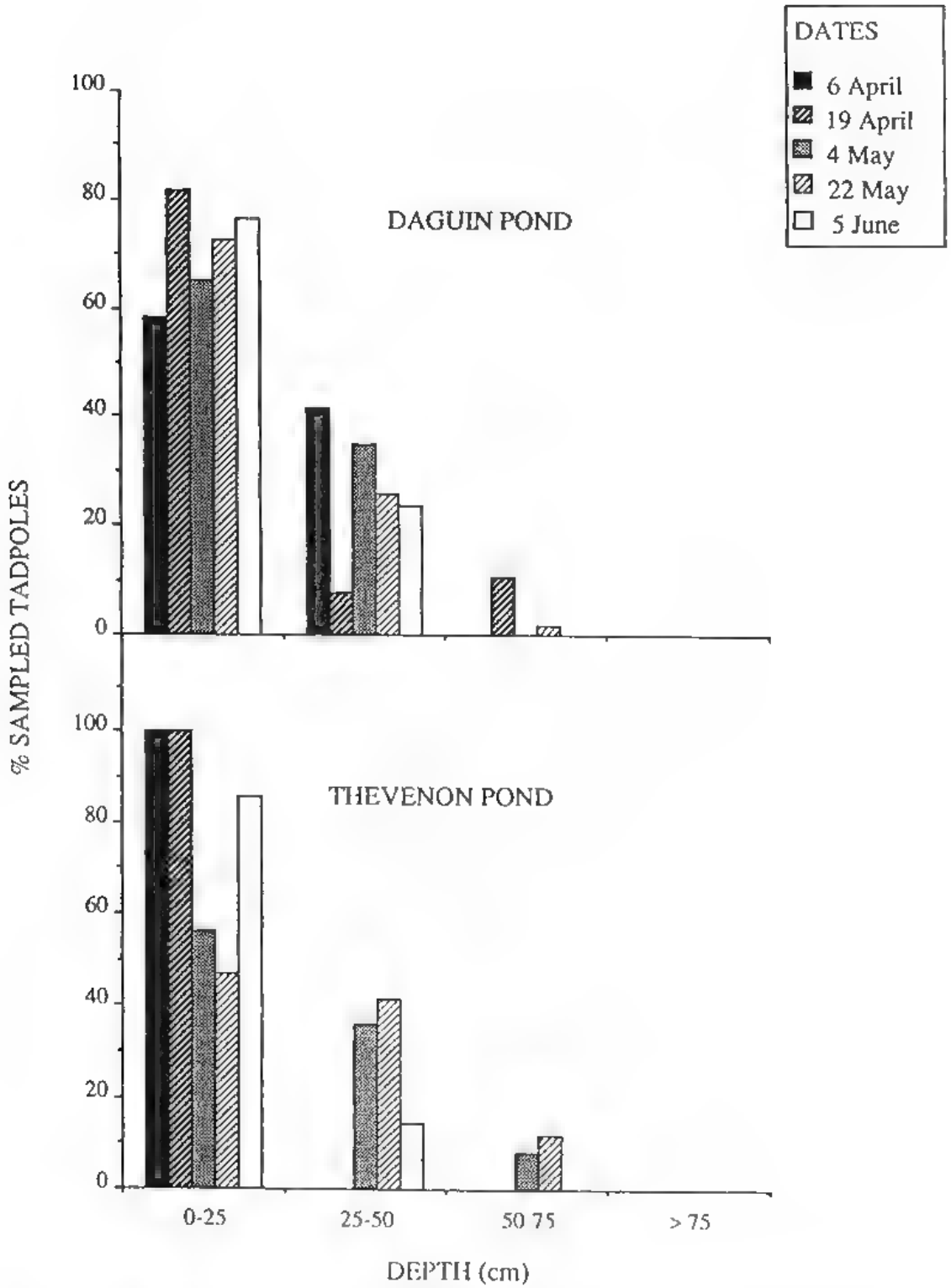

Fig 3. – Relationship between tadpole density (expressed in percentages) and water depth for the five sampling dates On the first date (6 April), tadpole dispersal has only begun in Daguin pond.

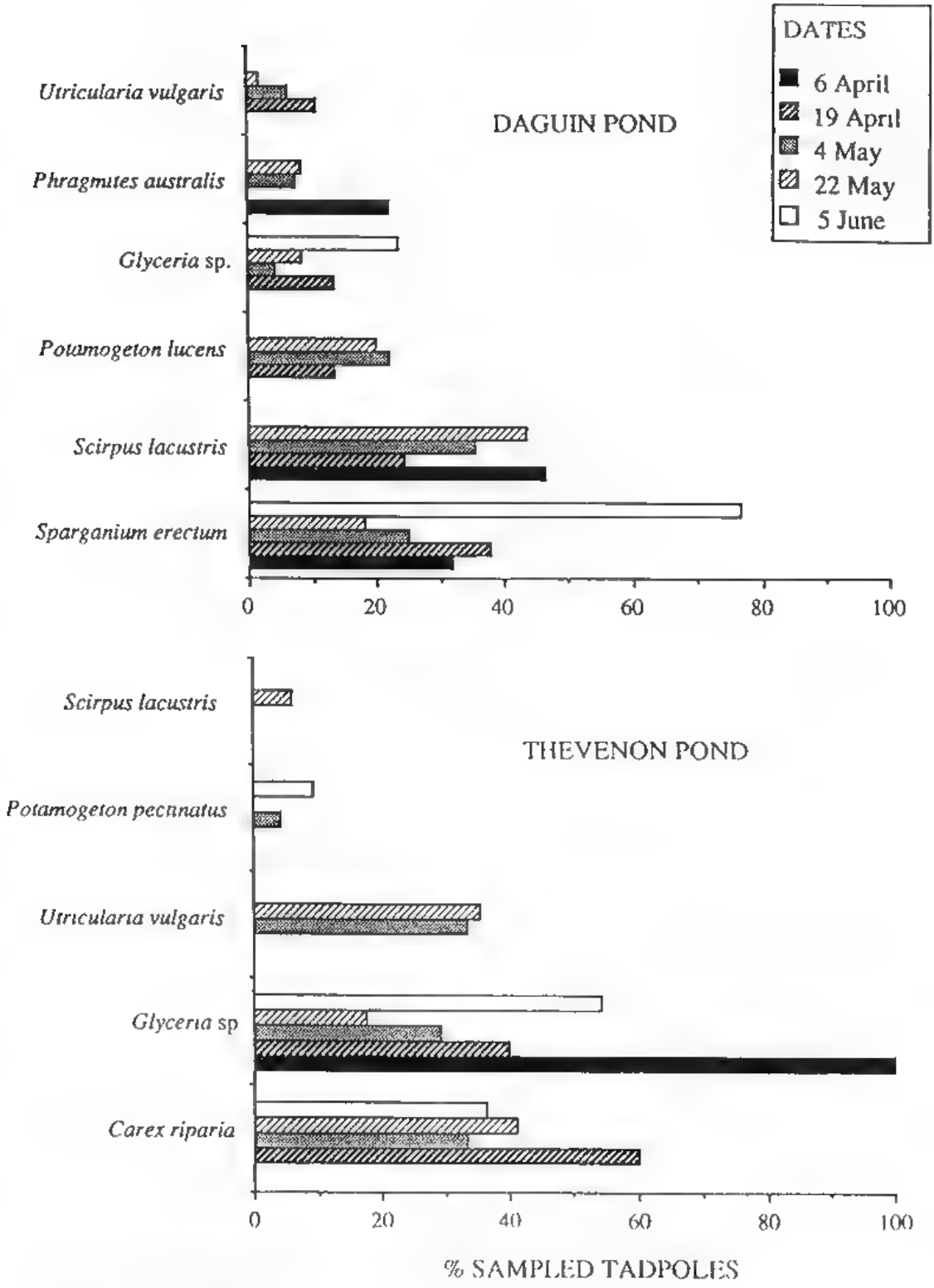

Fig. 4. Relationship between tadpole density (expressed in percentages) and plant species for the five sampling dates.

Another factor, not measured in our study, which might influence tadpole dispersion, was the presence of fishes which reached rather high densities in the two ponds (personal observations). Indeed, as fishes are known to prey heavily on tadpoles (BEEBEE, 1983; KATS, PETRANKA & SIH, 1988), they may restrict tadpole dispersion to the parts of the ponds where vegetation provides a refuge against predation (CLAUSNITZER, 1983).

Metamorphosis also occurred in pond tails. The presence of vegetation and a gentle slope may help to prevent tadpoles from drowning, what has been observed during metamorphosis in *R. temporaria* (SAVAGE, 1961; ASHBY, 1969). At Thévenon, froglets emerged on both sides of each of the two pond tails toward the forest At Daguin, the froglets left the pond on the side of the little wood which is adjacent to the fishpond tail. Emigration in that direction may be due to an attraction of froglets by forest. In contrast to KOSKELA's (1973) observations, metamorphosis occurred in sunny weather; hence movement toward the forest may ensure favourable conditions for froglet life (ASHBY, 1969). According to SMIRINA (1980), froglet mortality is the highest during the first weeks after metamorphosis. The hypothesis of an attraction of froglets by forest has to be tested experimentally.

RÉSUMÉ

La dispersion des têtards de grenouilles rousses (*Rana temporaria*) a été suivie depuis l'éclosion jusqu'à l'émergence, par un échantillonnage systématique en des points régulièrement distribués, dans deux grands étangs de Bresse jurassienne (Est de la France). Cette dispersion comporte deux phases successives. Au cours de la première phase, des bancs de têtards se dispersent depuis le site de frai dans différentes directions Ensuite, ces bancs se diffusent et les têtards colonisent les parties les moins profondes de l'étang. Il est remarquable qu'ils ne colonisent pas entièrement les rives, mais seulement les zones de queue d'étangs, zones de faible profondeur les plus vastes comportant une forte densité de végétation. Ils émergent du côté le plus ombragé de l'étang. Malgré de fortes différences de végétation, le mode et la dynamique de dispersion des têtards ne diffèrent pas entre les deux étangs

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